THE EFFECTS OF TEMPERATURE ON THE CHARACTERISTICS OF THE DOGFISH OCULOMOTOR SYSTEM

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SUMMARY

The dogfish oculomotor system can be modelled as a first order linear system (Montgomery, 1983) and hence can be specified by its characteristic frequency and gain. This paper describes the effect of temperature on these two parameters. The characteristic frequency is directly related to temperature, and decreases from 0·31 Hz at 20 °C to 0·15 Hz at 10 °C. The gain is inversely related to temperature, increasing approximately 2·5 times over a temperature drop from 20 °C to 10 °C. It is argued that the increase in gain with falling temperature can be attributed to an increase in relaxation time of the muscle, and that it is likely to be of biological significance in maintaining reflex performance in a poikilothermic animal.

INTRODUCTION

Most fish are poikilothermic; their body temperature closely matches environmental temperature. During seasonal fluctuations in water temperature, or during movement into a different water mass the fish are subject to considerable changes of body temperature.

Reflex activity in intact fish can be maintained over quite a wide range of temperature (Roots & Prosser, 1962; Friedlander, Kotchabhakdi & Prosser, 1976). The thermal sensitivity of muscle function has been studied in isolated neuromuscular preparations (Macdonald & Montgomery, 1982; Fischer & Florey, 1981; Putnam & Bennett, 1982). Over the range of animals studied the results are relatively consistent. As temperature is lowered, muscle twitch size and duration increase, as does muscle contraction in response to low stimulus frequencies. Maximal tetanic contraction, however, is best at higher temperatures.

The dogfish oculomotor system provides the opportunity to study the thermal sensitivity of a complete motor output pathway with the muscle operating *in situ* against its normal mechanical load. This whole system can be modelled as a first order linear system (Montgomery, 1983) and hence specified by its characteristic frequency and gain. In this study we describe the effect of temperature on these two properties and evaluate the significance of these results with respect to normal ocular reflex activity.

MATERIALS AND METHODS

Experiments were performed on the carpet shark *Cephaloscyllium isabella* caught in trawl nets, or on long lines, and kept in the seawater circulation at the Leigh Marine Laboratory. In fish anaesthetized with Tricaine (by immersion in a 0·02% solution in sea water), the cranium was opened and the brain removed leaving the stumps of the cranial nerves accessible intracranially. Fish were then placed in a tank and the gills perfused with sea water at the ambient temperature of 14 °C. The stump of the abducens nerve (cranial nerve VI) was secured in a suction electrode, and the cranial cavity filled with elasmobranch Ringer.

Stimuli were trains of supramaximal square wave pulses (0·5 ms, 1·5–2 V). Pulse trains were delivered at a constant frequency in the range 0–100 Hz, or sinusoidally modulated between 3–25 Hz at modulation frequencies in the range 0·05–2 Hz. Modulated spike trains were obtained by triggering from the frequency modulated output of a function generator.

Eye movements were recorded using a photodetector mounted in the film plane of a camera directed at a reflective patch on the eye. The position of the patch image on the detector was transduced to a voltage which was monitored on an oscilloscope and recorded on FM tape. At the conclusion of each experiment, the voltage output of the photodetector was calibrated to eye deflection. Recordings were initially made at the ambient temperature of around 14 °C. The temperature was first lowered to 10 °C and then raised to 20 °C. At each temperature, recordings were made after an equilibration period of about 1 h. During each recording sequence a 1-s 20-Hz standard pulse train was used to check that the response was not declining due to fatigue. In one experiment the long-term stability of the preparation was verified by returning it to 14 °C. The mean response of a series of test pulses was not significantly different from those obtained at the beginning of the experiment. One group of three fish was experimented on in the summer period when the ambient and recording temperatures were both close to 20 °C.

RESULTS

The response of one preparation to constant frequency pulse trains at two different temperatures is shown in Fig. 1. The latency of the response for all fish increased at low temperature, being 38 ± 7, 50 ± 6 and 63 ± 10 ms at 20, 14 and 10 °C respectively. The rate of muscle relaxation at the end of the stimulus pulse train was faster at high temperature (Fig. 1). The most striking effect of temperature was on the stimulus-response characteristics (Fig. 2). At 10 °C low frequencies of stimulation were quite effective in producing eye movement, and maximum eye deflection was produced by frequencies of about 40–50 Hz. At higher temperatures, low frequencies of stimulation were much less effective, and stimulus frequencies greater than 75 Hz were required to produce full eye deviation. The stimulus-response curves for all fish are shown in Fig. 2, the slopes of the stimulus-response curves increase at low temperature. The results for fish acclimated to 14 °C but recorded at 20 °C were quite similar to 21 °C recordings made from fish acclimated to this temperature.
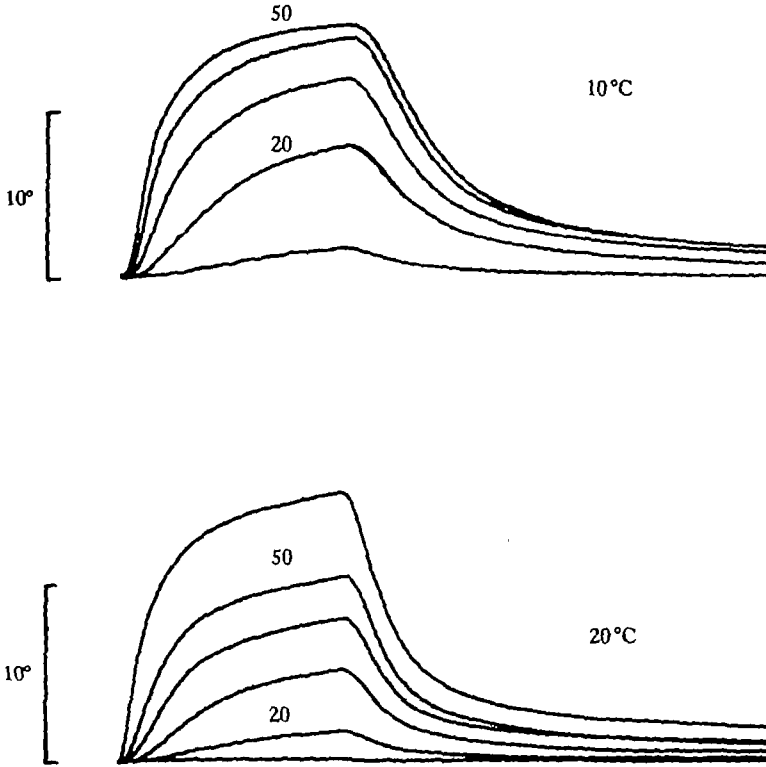
Fig. 1. Eye rotation produced by constant frequency pulse trains in one preparation at 10 °C and 20 °C. Note the decreased rate of relaxation at 10 °C. The duration of all pulse trains was 1 s, the responses to 20 Hz and 50 Hz are indicated. Note the increased response to 20 Hz at 10 °C and that at this temperature the response is close to saturating at 50 Hz.

Fig. 3 shows the response at 10 and 20 °C of one preparation to pulse trains sinusoidally modulated at frequencies between 0·05 and 2 Hz. The amplitude of the input sine wave was the same at both temperatures. The relative gain of the response was lower at 20 °C than at the lower temperature, and decreased as modulation frequency was raised. It is apparent in this example that the fall-off in gain was less at 20 °C, indicating a shift in the characteristic frequency. This result was verified by determining the characteristic frequency at each recording temperature by fitting the best first order model of the form:

$$G(f) = \frac{1}{\sqrt{1 + (f/f_c)^2}},$$

where G is relative gain; f_c is characteristic frequency and f is modulation frequency, determined by a non-linear regression technique (Helwig & Council, 1979). The characteristic frequencies were 0·15 ± 0·03 Hz at 10 °C, 0·18 ± 0·05 Hz at 14 °C and 0·31 ± 0·06 Hz at 20 °C (±95 % confidence values).

The relationship between gain and temperature is shown in Fig. 4. Three independent estimates of gain are plotted for each test temperature. The gain calculated from the height of the 20-Hz 20-pulse standard is likely to be an underestimate of gain (since
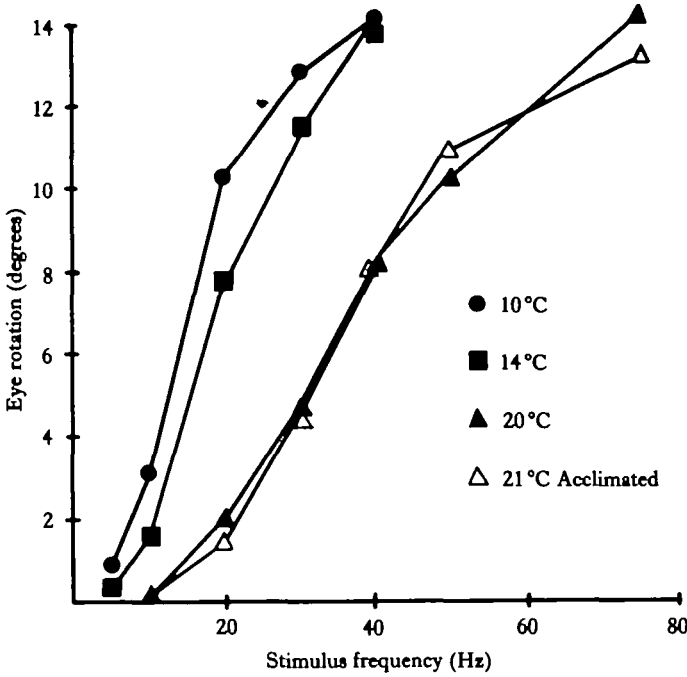
Fig. 2. Stimulus-response curves. Mean eye rotation (ordinate) produced by different stimulation frequencies (abscissa) for 14 °C acclimated fish recorded at 10, 14 and 20 °C. 21 °C acclimated fish recorded at 21 °C. Note the increased slope of stimulus response curves at low temperature.
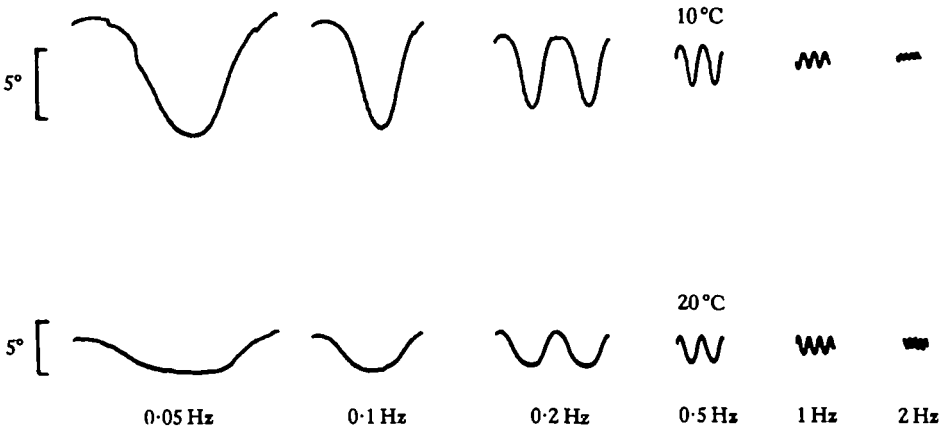

Fig. 3. Eye rotation produced by sinusoidally modulated pulse trains in one preparation at 10 °C and 20 °C (peak to peak amplitude 22 Hz, modulation frequency 0·05-2 Hz). Note the increased gain at low modulation frequency for the 10 °C response, and the tendency for the relative gain of the response at this temperature to fall off more rapidly as modulation frequency is increased.

the eye deflection was still increasing at the end of the train, see Fig. 1), but is included as about six replicates of the standard pulse were available for each fish at each test temperature, and these results clearly support the trends shown by the other two gain estimates. The slope of the stimulus response curve, and the amplitude ratio of low
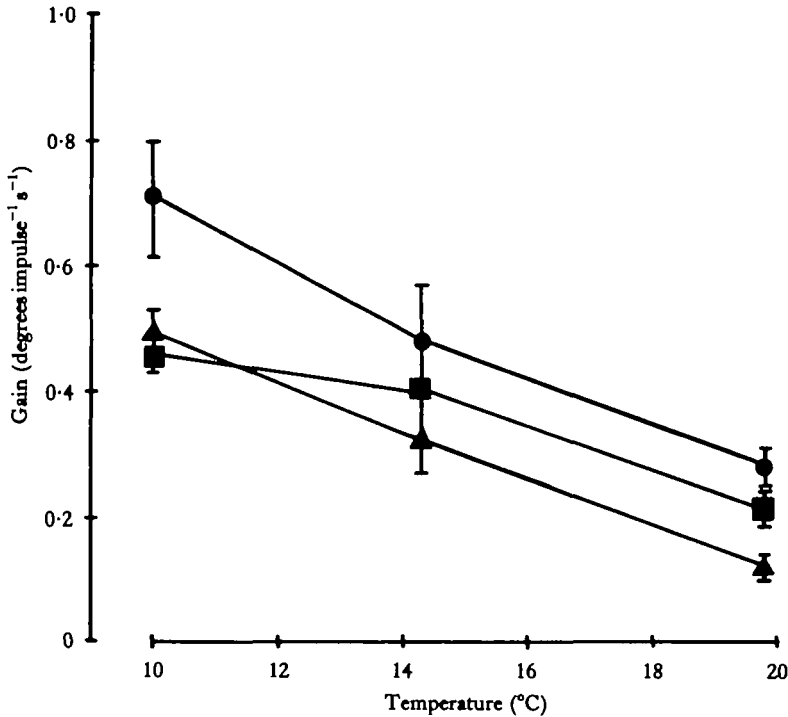
Fig. 4. Effect of temperature on gain. Three independent estimates of gain at three different record-ing temperature (mean ± standard deviation). Slope of stimulus-response curve (●); sine wave amplitude ratio (0·05 Hz, ■); height of 20-Hz 20-pulse standard (▲).

frequency sine wave inputs also provide estimates of the gain and both indicate an increase at low temperature. The overall mean increases from 0·2 at 20 °C to 0·4 at 14 °C and to 0·55 at 10 °C.

DISCUSSION

The inverse relationship between gain in the dogfish oculomotor system and tem-perature can be attributed to the effects of temperature on muscle twitch contraction. This is most clearly demonstrated in the recent study of Putnam & Bennett (1982) on the effects of temperature on contractile properties of lizard muscle. They showed that twitch amplitude did increase in some muscles on cooling, but that this effect was rather variable. Twitch duration, however, showed a strong and consistent increase as temperature was lowered. This result has also been shown in rat skeletal muscle (e.g. Close & Hoh, 1968) and so is not peculiar to poikilothermic animals. The effect of an increased twitch duration is to produce summation at lower frequencies, which considerably increases the slope of the stimulus-response curve. This result has been shown in mammalian muscle (Doudoumopoulos & Chatfield, 1959) and very convin-cingly in crayfish (Fischer & Florey, 1981). Its significance becomes apparent within the context of the oculomotor system where it produces a considerable increase in system gain at low temperature.

The characteristic frequency of the oculomotor system is determined by the viscous
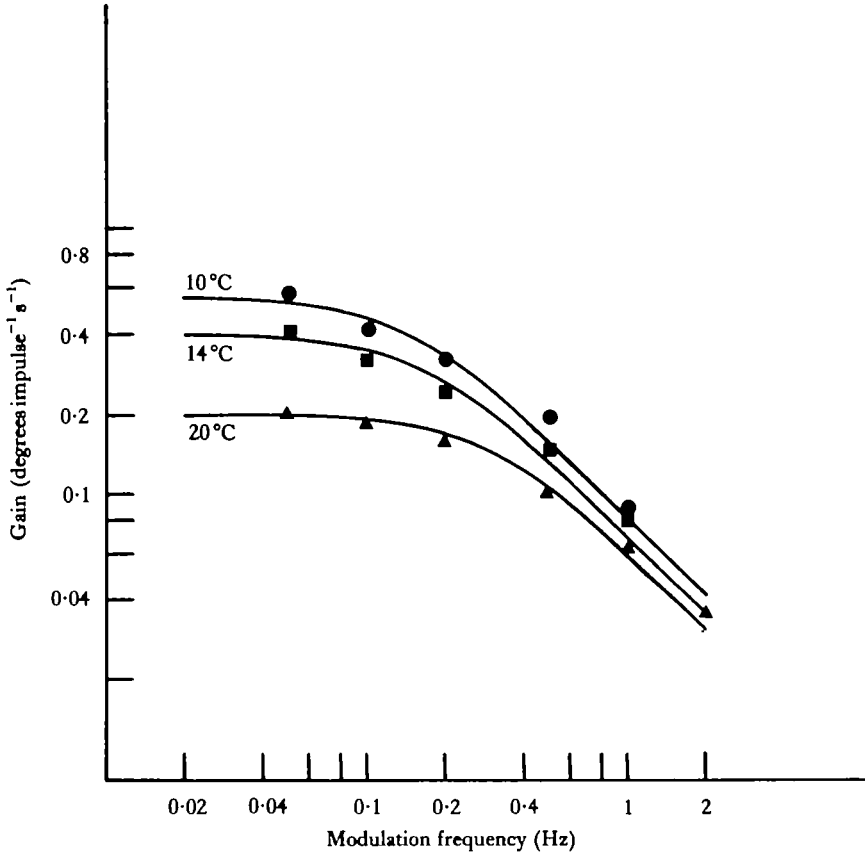
Fig. 5. Model of the oculomotor system at three different temperatures. Symbols represent the mean experimental response (●, 10 °C; ■, 14 °C; ▲, 20 °C), solid lines are the theoretical models whose respective static gains and characteristic frequencies are 0·55, 0·13 Hz; 0·4, 0·18 Hz; 0·2, 0·31 Hz. Note the difference in gain is less in the upper frequency range, say at 1 Hz, than it is at low modulation frequency.

coupling of the globe to the orbit (Collins, 1977). It is not surprising therefore that low temperature, which increases viscosity, should effectively lower the characteristic frequency. At the upper end of the natural frequency range for head movements (0·05–1 Hz approx.) the lower characteristic frequency will to some extent offset the increased gain at low temperature. This effect is illustrated in the calculated Bode plots for the three different temperatures (Fig. 5). The difference in gain at low modulation frequencies is reduced in the upper frequency range, because the high gain response at low temperature also has the lowest characteristic frequency.

The increased gain of the oculomotor system at low temperature is likely to be of biological significance. It has been demonstrated that the absolute refractory period is strongly temperature sensitive (e.g. Talo & Lagerspetz, 1967) and this clearly puts an upper bound on maximum CNS output. For instance the refractory period of antarctic fish nerves in the range 0–5 °C is about 15–25 ms, limiting the firing frequencies to about 40–60 Hz despite the long period of adaptation these fish have had to cold temperatures (Macdonald & Montgomery, 1982). The effect of temperature on the normal function of sense organs is not well understood. The direct effects o

temperature on sense organs were reported in many early studies, particularly at the time when the biological function of the sense organ was still in debate (e.g. Murray, 1956). What is more relevant here is the effect of temperature on the normal sensory transduction process; that is, the effects of temperature on sensory gain. This has been determined for the Pacinian corpuscle in mammals (Inman & Peruzzi, 1961) and the visual system in goldfish (Schellart, Sperkreijse & van den Berg, 1974), and in both cases gain decreases on cooling. Also of interest from the point of view of ocular reflexes is the theoretical prediction that the gain of semicircular canals in the vestibular system will decrease at low temperature due to the increased viscosity of the endolymph (Oman, 1981). It thus seems likely that sensory gain and CNS output will both decrease at low temperature. This will be offset to some extent by an increased gain in the motor output system, providing an elegant mechanism for automatic temperature compensation.

REFERENCES

CLOSE, R. & HOH, J. F. Y. (1968). Influence of temperature on isometric contractions of rat skeletal muscles. *Nature, Lond.* **217**, 1179–1180.

COLLINS, C. C. (1977). Orbital mechanics. In *The Control of Eye Movements*, (eds P. Bach-y-rita, C. C. Collins & J. Hyde), pp. 283–325. New York: Academic Press.

DOUDOUMOPOULOS, A. N. & CHATFIELD, P. O. (1959). Effects of temperature on function of mammalian (rat) muscle. *Am. J. Physiol.* **196**, 1197–1199.

FISCHER, L. & FLOREY, E. (1981). Temperature effects on neuromuscular transmission (opener muscle of crayfish, *Astacus leptodactylus*). *J. exp. Biol.* **94**, 251–268.

FRIEDLANDER, M. J., KOTCHABHAKDI, N. & PROSSER, C. L. (1976). Effects of cold and heat on behaviour and cerebellar function in goldfish. *J. comp. Physiol.* **112**, 19–45.

HELVERSON, O. N. & ELSNER, N. (1977). The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device. *J. comp. Physiol.* **122**, 53–64.

HELWIG, J. T. & COUNCIL, K. A. (1979). *The Statistical Analysis System User's Guide*. North Carolina: S.A.S. Institute.

INMAN, D. R. & PERUZZI, P. (1961). The effects of temperature on the responses of Pacinian corpuscles. *J. Physiol., Lond.* **155**, 280–301.

MACDONALD, J. A. & MONTGOMERY, J. C. (1982). Thermal limits of neuromuscular function in an antarctic fish. *J. comp. Physiol.* **147**, 237–250.

MONTGOMERY, J. C. (1983). Eye movement dynamics in the dogfish. *J. exp. Biol.* **105**, 297–304.

MURRAY, R. W. (1956). The thermal sensitivity of the lateralis organs of *Xenopus J. exp. Biol.* **33**, 798–805.

OMAN, C. M. (1981). The influence of duct and utricular morphology on semicircular canal response. In *The Vestibular System Function and Morphology*, (ed. T. Gualtierotti). New York: Springer-Verlag.

PUTNAM, R. W. & BENNETT, A. F. (1982). Thermal dependence of isometric properties of lizard muscle. *J. comp. Physiol.* **147**, 11–20.

ROOTS, B. I. & PROSSER, C. L. (1962). Temperature acclimation and the nervous system in fish. *J. exp. Biol.* **39**, 617–629.

SCHELLART, N. A. M., SPEKREIJSE, N. A. M. S. H. & VAN DEN BERG, T. J. T. P. (1974). Influence of temperature on retinal ganglion cell response and E.R.G. of goldfish. *J. Physiol., Lond.* **238**, 251–267.

TALO, A. & LAGERSPETZ, K. Y. H. (1967). Temperature acclimation of the functional parameters of the giant nerve fibres in *Lumbricus terrestris* L. II. The refractory period. *J. exp. Biol.* **47**, 481–484.